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Biogeographic Relationships of a Rocky Intertidal Fish Assemblage in an Area of Cold Water Upwelling off Baja California, Mexico[1]

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ABSTRACT: The rocky intertidal fish assemblage at an area of nearshore cold water upwelling at Punta Clara, northern Baja California, Mexico was sampled bimonthly for 1 yr. Temperatures in this upwelling region typically range from 10° to 16°C throughout the year and are significantly lower than those of surrounding areas in the warm-temperate Californian biogeographic province. The assemblage at Punta Clara is a species-rich mixture composed of eight fishes that are primarily Californian in distribution, seven that are primarily Oregonian cold-temperate, and four that range throughout both provinces. In terms of relative numbers, 53% of the total number of fishes are Californian, 33% are Oregonian, and 14% belong to both provinces. In terms of biomass, 75% are Californian, 20% are Oregonian, and 5% belong to both provinces. Two common intertidal fishes characteristic of the Californian province (and belonging to the largely tropical and subtropical families Blenniidae and Labrisomidae) are absent, as are members of the Stichaeidae, which are characteristic of the Oregonian intertidal. Populations of Oregonian fishes in these upwelling regions off Baja California may be Pleistocene relicts maintained by cold temperatures. Alternatively, allozyme studies of two of these species suggest considerable gene flow between northern and Baja Californian populations that could be maintained by larval transport in coastal currents, such as the California Current.

POINT CONCEPTION, CALIFORNIA (34.5° N) forms a boundary or transitional zone between the warm-temperate Californian biogeographic province to the south (a region that extends to ca. 25° N, Baja California, Mexico) and the cold-temperate Oregonian province to the north (Garth 1955, Valentine 1966, Brusca and Wallerstein 1979). Nearshore surface waters in the Californian province typically have temperatures ranging from 13° to 21°C throughout the year, whereas those at Point Conception range from 11.5° to 14°C, and those in the Oregonian province range from 9° to 12°C (see Table 1; Hubbs 1948, 1960, 1961, 1962, 1963).

Point Conception is the southern limit of the ranges of many species, including fishes, of the Oregonian province (Horn and Allen 1978). However, several nearshore fishes (Hubbs 1948, 1960), invertebrates (Garth 1955), and algae (Dawson 1960) that are distributed primarily in the Oregonian province reappear in localized nearshore areas of cold water upwelling off northern Baja California, Mexico (Hubbs 1948, 1960). These Oregonian species largely skip the warmer waters of southern California and coexist with many of the Californian biota in these upwelling regions (Hubbs 1948, 1960, Dawson 1960, Briggs 1974). The upwelling areas have surface temperatures 3° to 9°C lower than those of immediately adjacent areas characteristic of the Californian warm-temperate biogeographic province (Hubbs 1948, 1960; see Table 1). The unique mixture of biota in these

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TABLE 1

TEMPERATURE DATA FOR PUNTA CLARA AND COMPARISON AREAS*

	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.	MEAN
Punta Clara, Baja California, Mexico; 31° 31.9′ N, 116° 39.7′ W													
1960	xxxx**	11.4	12.2	12.9	12.6	xxxx	15.6	15.0	15.2	14.6	16.8	16.6	14.3
1961	14.4	13.4	13.5	13.8***	15.9	13.6	14.7	14.7***	14.9	xxxx	xxxx	xxxx	14.3
1962	14.6	12.7	12.0	xxxx	13.4***	xxxx	17.0	14.6	15.6	16.9	12.6	14.4	14.4
1963	13.1	12.2	12.8	xxxx	12.5	14.5	14.9	16.5***	16.7	xxxx	14.4	xxxx	14.2
Mean	14.0	12.4	12.6	13.3	13.6	14.0	15.6	15.2	15.6	15.8	14.6	15.5	14.35
La Jolla, Scripps Pier, California; 32° 52.0′ N, 117° 15.3′ W													
1961	13.8	12.6	16.2	xxxx	18.9	17.5	17.7	18.9	18.7	xxxx	xxxx	xxxx	16.8
1962	13.4	14.7	15.5	xxxx	17.6	xxxx	20.0	20.8	18.5	18.7	14.7	14.3	16.8
1963	13.2	12.5	15.2	xxxx	15.7	17.2	13.6	21.4	17.7	xxxx	14.8	xxxx	15.7
Mean	13.5	13.3	15.6	xxxx	17.4	17.4	17.1	20.4	18.3	18.7	14.8	14.3	16.44
Pt. Piedras Blancas, Eastern Point, California; 35° 39.9′ N, 121° 15.6′ W													
1961	12.1	12.2	12.2	11.4	12.5	14.2	13.2	14.7	14.8	13.0	13.9	13.0	13.1
1962	14.0	12.1	11.5	12.0	11.8	12.1	14.4	14.5	14.3	14.0	11.7	12.8	12.9
1963	11.3	12.5	11.7	12.2	11.6	12.6	13.8	13.2	14.3	14.1	12.5	13.3	12.8
Mean	12.5	12.3	11.8	11.9	12.0	13.0	13.8	14.1	14.5	13.7	12.7	13.0	12.94
Mendocino, California; 39° 18.2′ N, 123° 48.2′ W													
1960	10.9	10.6	9.7	10.1	10.0	9.9	10.1	10.0	10.7	11.6	11.2	11.6	10.5
1961	11.7	11.2	10.3	9.4	9.8	10.5	10.4	11.6	11.4	11.8	10.8	11.0	10.8
1962	10.4	10.8	10.1	9.1	9.0	9.0	10.2	11.1	11.0	11.8	11.2	11.1	10.4
Mean	11.0	10.9	10.0	9.6	9.6	9.8	10.2	10.9	11.0	11.7	11.1	11.2	10.58

* Based on Hubbs 1960, 1961, 1962, 1963.
** xxxx = missing data.
*** Multiple readings for that month.

upwelling areas and their disjunct distribution patterns have been little studied to date.

In the present study, we examined the intertidal fish assemblage at an upwelling site off Punta Clara, Baja California, Mexico (31° 31.9′ N, 116° 39.7′ W; 55 km SW of Ensenada, Mexico; Figure 1) to provide baseline data for analyzing these patterns of distribution. This site was the location of a long-term study of temperature by Hubbs (1960; see Table 1). In the present study, we compared results from 1 yr of bimonthly sampling with data from intertidal fish assemblages from the Oregonian and Californian biogeographic provinces. It is part of a larger investigation of gene flow between these disjunct populations of nearshore fishes.

MATERIALS AND METHODS

Fishes were collected bimonthly during minus tides for 1 yr (October 1988 through September 1989) from tide pools located at the water's edge, having abundant algae, and ranging to 1.5 m Mean Lower Low Water (MLLW) in maximum depth using the anesthetic quinaldine sulphate. Collections began ca. 45 min before the lowest point of the tide and extended to 1 hr after. All fishes seen were netted by three to five collectors (including some with snorkel gear) and immediately frozen on dry ice for later laboratory analysis. Sample dates and tide levels were as follows: 23 October 1988 (−0.5 m MLLW), 22 December 1988 (−1.5 m MLLW), 17 February 1989 (−1.0 m MLLW), 9 April 1989 (0.0 m MLLW), 6 June 1989 (−1.2 m MLLW), and 19 August 1989 (−0.3 m MLLW). Temperatures at the water's edge (not in isolated tide pools) ranged from 10.5°C (February 1989) to 14.5°C (December 1988).

Total lengths (TL) of fishes to the nearest millimeter and weights to the nearest 0.5 g were measured as soon as possible after collection. Determination of primary biogeographic ranges of the intertidal fishes was based on data from Hubbs (1948), Williams (1957),

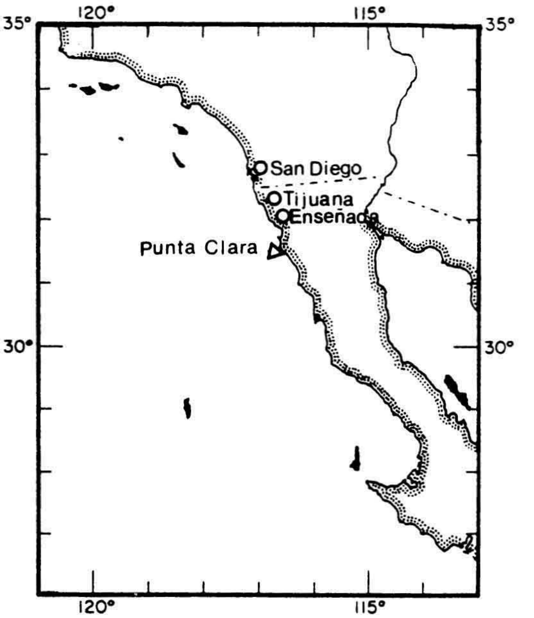

FIGURE 1. Location of study site: Punta Clara, Baja California, Mexico.

Miller and Lea (1972), Burge and Schultz (1973), Fitch and Lavenberg (1975), Davis (1977), Horn and Allen (1978), Yoshiyama (1980, 1981), Grossman (1982, 1986), Allen (1985), Eschmeyer et al. (1983), Moring (1986), Stepien (1986, 1991*a*,*b*), Wells (1986), Yoshiyama et al. (1986), Matson et al. (1986), Ruiz-Campos and Hammann (1987), Stepien et al. (1988), Stepien and Rosenblatt (1991), and from R. H. Rosenblatt (pers. comm., 1989). Results of the present study were compared with those of other studies of intertidal fishes from the Californian and Oregonian biogeographic provinces.

RESULTS

Relative Abundances and Biomass

A total of 516 individuals from 19 species and seven families was collected at Punta Clara. Number of individuals per species per collection, predominant biogeographic province(s), biomass (total weight), and size range are given in Table 2. The most common rocky intertidal fishes were (in decreasing order of relative abundance): spotted kelpfish, *Gibbonsia elegans* (Clinidae; 22.5% of the total number collected); woolly sculpin, *Clinocottus analis* (Cottidae; 19.8% of the total); crevice kelpfish, *Gibbonsia montereyensis* (Clinidae; 12.4%); rosy sculpin, *Oligocottus rubellio* (Cottidae; 10.1%); striped kelpfish, *Gibbonsia metzi* (Clinidae; 7.9%); and opaleye, *Girella nigricans* (Girellidae; 7.9%) (Figure 2). Thirteen fishes were less common, including (in decreasing order of relative abundance): the rockweed gunnel, *Xererpes fucorum* (Pholididae); smoothhead sculpin, *Artedius lateralis* (Cottidae); fluffy sculpin, *Oligocottus synderi* (Cottidae); reef surfperch, *Micrometrus aurora* (Embiotocidae); spotted snailfish, *Liparis florae* (Liparididae); California clingfish, *Gobiesox rhessodon* (Gobiesocidae); coralline sculpin, *Artedius corallinus* (Cottidae); dwarf surfperch, *Micrometrus minimus* (Embiotocidae); cabezon, *Scorpaenichthys marmoratus* (Cottidae); black surfperch, *Embiotoca jacksoni* (Embiotocidae); slender clingfish, *Rimicola eigenmanni* (Gobiesocidae); and shiner surfperch, *Cymatogaster aggregata* (Embiotocidae) (Figure 2 and Table 2).

Relative frequencies and contributions to the total biomass for all species are compared in Figure 2. *Girella nigricans* had the greatest cumulative weight of a species (37.4% of the total of all fishes), followed by *Clinocottus analis* (21.4%), *Gibbonsia metzi* (12.43%), and *G. elegans* (11.6%; Figure 2). These four species accounted for 5614 g (82.8%) of the 6776 g total weight of all fishes. *Heterostichus rostratus* reached the largest size (TL), followed by *Girella nigricans* and *Gibbonsia metzi.*

Biogeographic Affinities

Eight species, including the two most common at Punta Clara (*Gibbonsia elegans* and *Clinocottus analis*), occur predominantly in the warm-temperate Californian biogeographic province, south of Point Conception (Table 2). Four species, including three cottids (and the fourth most abundant species, *Oligocottus rubellio*), are found in both the Californian and Oregonian provinces. Seven species, including the third and fifth most

TABLE 2

NUMBER OF EACH SPECIES PER COLLECTION, PREDOMINANT BIOGEOGRAPHIC PROVINCE(S), SIZE RANGE, AND BIOMASS (TOTAL WEIGHT OF EACH SPECIES, g)

FAMILY	SPECIES	PREDOMINANT BIOGEOGRAPHIC PROVINCE(S)*	SIZE RANGE (TL, mm)	TOTAL WEIGHT (g)	NUMBER PER COLLECTION**						TOTAL NO. COLLECTED
					1	2	3	4	5	6	
Clinidae	*Heterostichus rostratus*	Ca.	238–274	268.3	1	—	1	—	—	—	2
	Gibbonsia metzi	Ore.	51–202	842.3	4	6	10	2	4	15	41
	Gibbonsia montereyensis	Ore.	33–85	163.9	2	38	17	4	—	3	64
	Gibbonsia elegans	Ca.	28–133	785.2	21	7	17	11	40	20	116
Cottidae	*Scorpaenichthys marmoratus*	Ca./Ore.	112–130	84.7	1	2	—	—	—	—	3
	Artedius corallinus	Ore.	46–64	11.7	1	1	2	—	—	—	4
	Artedius lateralis	Ore.	43–111	148.7	2	6	8	—	3	2	21
	Oligocottus snyderi	Ca./Ore.	36–77	43.6	5	1	1	—	1	8	16
	Oligocottus rubellio	Ca./Ore.	40–101	205.8	—	18	9	3	12	10	52
	Clinocottus analis	Ca.	39–150	1,452.5	32	16	6	18	14	16	102
Embiotocidae	*Cymatogaster aggregata*	Ca.	45	1.1	—	—	—	—	1	—	1
	Embiotoca jacksoni	Ca.	42–106	23.5	—	1	1	—	—	—	2
	Micrometrus minimus	Ca./Ore.	54–80	19.5	3	—	1	—	—	—	4
	Micrometrus aurora	Ore.	63–100	75.6	—	5	6	—	—	—	11
Gobiesocidae	*Rimicola eigenmanni*	Ca.	31	0.3	—	—	—	—	1	—	1
	Gobiesox rhessodon	Ca.	30–50	7.8	3	—	1	2	—	—	6
Girellidae	*Girella nigricans*	Ca.	54–215	2,534.0	—	12	26	—	3	—	41
Liparididae	*Liparis florae*	Ore.	33–55	7.3	4	1	1	1	—	—	7
Pholididae	*Xererpes fucorum*	Ore.	71–136	100.2	7	7	2	2	2	2	22
Totals				6,776.0	86	121	109	43	81	76	516

*Ca. = Californian Province, Ore. = Oregonian province.
**Collection 1 = October 1988, Collection 2 = December 1988, Collection 3 = February 1989, Collection 4 = April 1989, Collection 5 = June 1989, Collection 6 = August 1989.

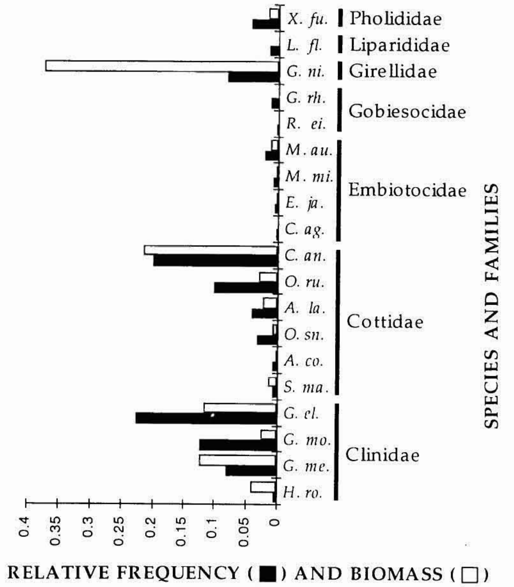

FIGURE 2. Percentage number ($n = 516$ fish) and percentage biomass (weight, g) for each species. Clinidae: *H. ro.* = *Heterostichus rostratus*, *G. me.* = *Gibbonsia metzi*, *G. mo.* = *G. montereyensis*, *G. el.* = *G. elegans*; Cottidae: *S. ma.* = *Scorpaenichthys marmoratus*, *A. co.* = *Artedius corallinus*, *O. sn.* = *Oligocottus snyderi*, *A. la.* = *Artedius lateralis*, *O. ru.* = *Oligocottus rubellio*, *C. an.* = *Clinocottus analis*; Embiotocidae: *C. ag.* = *Cymatogaster aggregata*, *E. ja.* = *Embiotoca jacksoni*, *M. mi.* = *Micrometrus minimus*, *M. au.* = *M. aurora*; Gobiesocidae: *R. ei.* = *Rimicola eigenmanni*, *G. rh.* = *Gobiesox rhessodon*; Girellidae: *G. ni.* = *Girella nigricans*; Liparididae: *L. fl.* = *Liparis florae*; Pholididae: *X. fu.* = *Xererpes fucorum*.

common (*Gibbonsia montereyensis* and *G. metzi*), are predominantly distributed in the cold-temperate Oregonian province, north of Point Conception (Table 2).

Warm-temperate fishes belonging to the Californian province composed 53.3% (275 individuals) of the total number of individuals. Cold-temperate Oregonian fishes composed 32.9% (170 individuals), and those widely distributed throughout both regions made up 13.8% (71 individuals) of the total number. In terms of biomass (relative to the total weight of all fishes), 74.9% (50,722.7 g) were Californian, 19.9% (1349.7 g) were Oregonian, and 5.2% (353.6 g) belonged to both provinces.

Seasonal Differences in Abundance

A greater number of species (17 of the 19) and individuals (44.6% of the yearly total) were collected during winter months (from 22 December 1988 and 17 February 1989) than at other times. Members of the family Clinidae were most numerous in winter (composing 42.1% and 41.3%, respectively, of the total number of individuals in the two winter samples). *Gibbonsia montereyensis* was the most abundant clinid in winter; however, *G. elegans* was more numerous in all other months and in yearly totals. Members of the family Cottidae were second in overall abundance during winter. *Oligocottus rubellio* was the most common cottid in winter, but was less common than *Clinocottus analis* in other months as well as in yearly totals (Table 2).

Fewer species (13 of 19 = 68.4%) and individuals (124 = 24% of the yearly total) were collected in spring (from 9 April 1989 and 6 June 1989) than in winter months. In both seasons, members of the family Clinidae were most numerous (39.5% of the total number of individuals collected in April and 54.3% in June). However, *Gibbonsia elegans* was the most common clinid in spring, followed by *G. metzi*. Members of the family Cottidae were also second in abundance, but *Clinocottus analis* was more common than *Oligocottus rubellio* (Table 2).

Fourteen species (73.7% of the total) and 162 individuals (31.4% of the total) were collected in summer (19 August 1989) and fall (23 November 1989). Clinidae also was the most abundant family collected in summer (50% of the total number of individuals), but members of the Cottidae were more abundant in fall (47.6%). The cottid *Clinocottus analis* was the most numerous species collected in summer and fall, followed by the clinid *Gibbonsia elegans* (Table 2).

DISCUSSION

The rocky intertidal fish assemblage in the nearshore upwelling area at Punta Clara, Baja California is a species-rich mixture of fishes characteristic of both the northern cold-temperate (Oregonian) and southern warm-temperate (Californian) biogeographic provinces (Table 2). Seven of the 19 species are primarily Oregonian in distribution (Yoshiyama 1981, Grossman 1982, 1986, Yoshiyama et al. 1986) and are largely absent from the Californian biogeographic province. Eight of the 19 species are primarily Californian in distribution, and four are widely distributed throughout both provinces (Table 2). The two most common species, *Gibbonsia elegans* and *Clinocottus analis*, are Californian and also were the most abundant in studies of other Californian rocky intertidal assemblages (Williams 1957, Allen 1985, Ruiz-Campos and Hammann 1987, Stepien 1991*a*). Species from the Californian province dominated collections in the present study, in both relative numbers and percentage biomass. Intertidal fishes characteristic of most collections in the Californian province, but absent from collections at Punta Clara, include the labrisomid *Paraclinus integripinnis* and the combtooth blenny, *Hypsoblennius gilberti* (Williams, 1957, Allen 1985, Ruiz-Campos and Hammann 1987, Stepien 1991*a*), which belong to families that are primarily tropically-subtropically distributed (Stephens and Springer 1972) and presumably are more stenotopic.

The clinids *Gibbonsia montereyensis* and *G. metzi* (which are two of the six most common species) are members of the Oregonian province that also occur in scattered cold-water areas in the Californian province. The southern populations, including those at Punta Clara, show little genetic isolation from populations north of Point Conception (Stepien and Rosenblatt 1991). These clinids have a long planktonic larval life (ca. 2 months; Stepien 1986, Stepien et al. 1988), and collection records suggest that they are readily transported by offshore currents, such as the California Current (H. G. Moser, National Marine Fisheries Serv., pers. comm., 1989). Davis (1977) showed that *G. metzi* and *G. montereyensis* are more cold-tolerant and less warm-tolerant than *G. elegans*. Seasonality in our collection records may suggest that *G. montereyensis*, which is the least warm-tolerant of the genus (Davis 1977), may move into deeper, cooler waters off Punta Clara during warmer months.

Temperatures at Punta Clara approximate those found in the transitional zone at Point Conception (see Table 1). They are slightly higher than those typical of Point Piedras Blancas, California (35°39.9′ N; Table 1). The species composition at Punta Clara resembles that at the transitional zone near Point Conception (Matson et al. 1986). For example, the southern Californian species *Girella nigricans* is common at San Simeon (Matson et al. 1986), and *Gibbonsia elegans* is collected occasionally (Stepien and Rosenblatt 1991).

Members of the Oregonian province found at Punta Clara include the cottids *Artedius lateralis* and *A. corallinus*, the embiotocid *Micrometrus aurora*, the liparidid *Liparis florae*, and the pholidid *Xererpes fucorum*. Cottids (Washington 1981, Washington et al. 1984), pholidids (Materese et al. 1984), and liparidids (H. J. Walker, Scripps Institution of Oceanography, pers. comm., 1989) have planktonic larvae that may be transported long distances by offshore currents. Marliave (1986) found that *Artedius* spp. larvae have relatively high offshore dispersal relative to that of other intertidal species. In contrast to intertidal samples in the Oregonian province (Grossman 1982, Matson et al. 1986, Moring 1986, Yoshiyama et al. 1986), stichaeids and the cottid *Oligocottus maculosus* were absent and the cottid *Oligocottus snyderi* was less common at Punta Clara.

Species richness at Punta Clara is higher than in typical intertidal collections in the Californian province (Williams 1957, Allen 1985, Ruiz-Campos and Hammann 1987, Stepien 1991*a*) and is similar to that of the Oregonian province (Grossman 1982, Matson et al. 1986, Moring 1986, Yoshiyama et al. 1986). Intertidal fish collections (with comparable sample sizes) in the Californian province typically number from 8 to 10 species (Williams 1957, Ruiz-Campos and Hammann 1987, Stepien 1991*a*). The Oregonian province typically has a greater number of species: for example; 17 species were collected at Dillon Beach, California by Grossmann (1982), 14 species at Dillon Beach by Yoshiyama et al. (1986), 18 species at Pescadero

Point, California by Yoshiyama et al. (1986), 11 at Cape Mendocino, California by Yoshiyama et al. (1986), and 14 at Cape Aragoo, Oregon by Yoshiyama et al. (1986). There may be fewer temperate species able to tolerate the warmer intertidal temperatures typical of the Californian province. Total area of rocky intertidal habitat and algal diversity and abundance (which provide refuge for both intertidal fishes and the small crustaceans that are their primary food source) are greater in the Oregonian province (Abbott and Hollenberg 1976, Grossman 1982, 1986, Newman 1979), which may increase fish diversity. Intertidal species characteristic of the Californian province but absent from the upwelling area (*Paraclinus integripinnis* and *Hypsoblennius gilberti*) may be particularly stenotopic and unable to tolerate the cooler temperatures found at Punta Clara. Study of environmental temperature tolerances of these species is necessary to address these questions.

The disjunct distribution pattern of cold-temperate Oregonian fishes, north of Point Conception and in the upwelling regions off Baja California, may be explained by two alternative hypotheses. Pleistocene fossil remains in the Californian province of fishes with present-day Oregonian distributions may suggest that their distributions (and cooler seawater temperatures) once extended further south (Hubbs 1948, 1960, Fitch 1967). Warming of the southern Californian province may have isolated these southern populations, which have been maintained by cold water upwelling.

Stepien and Rosenblatt (1991) examined genetic differentiation between populations north of Point Conception and at Punta Clara (as well as other locations) of two of these predominantly Oregonian intertidal fishes (*Gibbonsia montereyensis* and *G. metzi*). Their results demonstrated high levels of gene flow and negligible genetic isolation for these disjunct populations.

These population relationships may be due to transport of pelagic fish larvae by coastal currents, such as the California Current (see Waples and Rosenblatt 1987 and Stepien and Rosenblatt 1991). Postlarval survival of cold-temperate Oregonian fishes may be lower in the warmer waters of southern California, whereas the upwelling areas off the southern ends of points along Baja California may provide suitable habitats. This may explain rarity of these northern species in the warm-temperate waters of southern California and their reappearance in upwelling areas, such as at Punta Clara. A combination of both hypotheses may be responsible for these unusual tide pool assemblages. Longstanding breeding populations may be supplemented by pelagic recruits. Further study of the population genetics, distribution patterns, and fossil record of these intertidal fishes is necessary to address these hypotheses.

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